REPRODUCTIVE SUCCESS OF THE WOOD THRUSH IN A DELAWARE WOODLOT¹

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Woodland habitat in northern Delaware is being altered considerably by urbanization (Catts et al., 1966). These habitat changes are not confined to Delaware but encompass most of the Atlantic seaboard. Changes in land-use priorities stemming from the increasing human population are resulting in the destruction of wooded areas. To evaluate the effects of these changes on wildlife populations, an ecological study of suburban woodlots is under way in the Department of Entomology and Applied Ecology at the University of Delaware.

Birds, being conspicuous and common, seemed a logical choice on which to undertake studies. Initially a 35.6-acre relatively undisturbed woodlot was chosen as a basic study unit so that a base line of breeding bird success could be established. Information gained on this unit is to be used for comparative purposes with breeding bird success obtained for greatly disturbed, remnant woodlots scattered throughout suburban developments.

This paper deals only with the Wood Thrush (*Hylocichla mustelina*) in the 35.6-acre study unit. In addition to the standard information on breeding success; i.e., per cent of nests successful, per cent of eggs hatching, per cent of young fledging, etc., an attempt is made to relate reproductive success to the interplay of the physical and biological factors at work in the woodlot. An analysis of the 142 Wood Thrush nesting attempts recorded over a two-year period is presented.

METHODS

Systematic nest searches were initiated in mid-May, 1965, and in late April in 1966. Searches were continued through mid-August. Grid lines located at 150-ft intervals were traversed at least once every three days except for a two-week period in July, 1965. As nests were located the following information was noted: plant species in which the nest was located, nest height above ground level, degree of nest completion, and number of eggs and young. Data on eggs and nestlings and their development were recorded until each nest was vacated. Heights of nests above ground were measured to the nearest half-foot. The contents of high nests were observed, using a mirror attached to a 10-foot length of ³/₄-inch thin-wall conduit.

Forty-six Wood Thrushes were banded and handled a total of 84 times during a concurrent netting operation that was conducted for approximately 36 hours every 2-3 weeks in the 1966 breeding season. The birds were weighed and measured, and when possible they were sexed and aged. This was the continuation of a less regular

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banding effort carried on by J. T. Linchan of the U. S. Fish and Wildlife Service in the study woodlot during the previous 10 years.

Vegetation of the study area was sampled in three ways. A tally of all overstory tree species two inches DBH (diameter breast height) and above was made on 40 per cent of the study area using a 66 foot wide strip transect. Line-intercept transects (10 m in length) were employed to measure understory shrub and sapling tree species, while 0.25 m² plots were used to sample herbs.

Climatological data were obtained from the records of the U.S. Department of Commerce for the Greater Wilmington Airport official weather station located approximately six miles from the study area.

STUDY AREA

Physical Features.—The study area is located within the eity limits of Newark, Delaware, on the University of Delaware Agricultural Experiment Station Farm. The wooded area is mitten-shaped, covering 35.6-acres. The topography is slightly hilly with a slope from north to south. Elevations range from 77 to 103 fect above sea level. Soils are variable, with loam, silt loam, and sandy loam represented. An intermittent stream drains the lower portions of the area.

Weather.—The average monthly temperature varied, but precipitation readings during 1965 and 1966 were all well below the long-term normal. Although a cold, damp period (13–19 June) occurred during the 1965 breeding season, neither Wood Thrush eggs nor nestlings appeared to have been affected by the inclement weather. However, two rain storms accompanied by strong winds on 10 June and 21 July 1966, blew a few nests to the ground.

Vegetation.—The study area is located near the fall line between the Piedmont Region and Coastal Plain, and consequently includes plant species common to both physiographic areas.

Two relatively distinct vegetational types, based on species composition and related to site and soils, were recognized; an upland type (23.2 acres) and a lowland type (12.4 acres).

The upland type was well stocked with 121 ft² basal area per acre and 322 stems per acre. Overstory trees present in the upland type included tulip poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), oaks (*Quercus spp.*) and hickories (*Carya spp.*). Flowering dogwood (*Cornus florida*), an important nest site species, accounted for little basal area but ranked sixth in number of stems. Tree diameters were rather evenly distributed among size classes. Predominant understory species were sweet pepperbush (*Clethra alnifolia*), blue beech (*Carpinus caroliniana*), spicebush (*Lindera benzoin*), arrowwood (*Viburnum dentata*), Japanese honeysuekle (*Lonicera japonica*) and Virginia creeper (*Parthenocissus quinquefolia*). The principal herbaceous plants in the upland type were mayapple (*Podophyllum peltatum*), false Solomon's seal (*Smilacina racemosa*), and enchanter's nightshade (*Circaea quadrisulcata*).

Much of the lowland type was even-aged secondary growth but with scattered mature red maples (Acer rubrum), sweet gums and pin oaks (Quercus palustris). The basal area per acre (130 ft²) was relatively high because of the large, mature trees. There were 390 stems per acre with secondary growth accounting for much of this total. Predominant understory plants included spicebush, arrowwood, sweet pepperbush, greenbrier (Smilax spp.), and Japanese honeysuckle. Herbs commonly found in the lowland type were mayapple, jack-in-the-pulpit (Arisaema triphyllum), touch-me-not (Impatiens biflora), and skunk cabbage (Symplocarpus foetidus). Plant names follow Gleason and Cronquist, 1963.



FIG. 1. Three point floating average curves for the daily number of active Wood Thrush nests, 1965-1966.

NESTING SEASON

Peaks of nesting activity.—The duration of use for any given active nest was approximately 30 days. Included in this 30-day period were 3–4 days for nest-building, 2–5 days for egg-laying, 13–14 days for incubation and 12–13 days for nestling growth before fledging. Nest-building was usually completed in four days but on one occasion extended for eight days. Brackbill (1958) states that generally the nest is complete after three days, but that some building may occur even up to seven days. Weaver (1939) reported that about five days were required for nest building in New York.

Interpolation and extrapolation of the nest survey data revealed the approximate day of initiation and termination of each nest. From these data the number of nests active on each day of breeding seasons (Fig. 1) was determined. The earliest active nest was started on 14 May and the latest on 13 July and vacated on 12 August. The primary nesting peak in both years occurred during the last two weeks of May, and a secondary peak was attained in the second week of July. Although the number of nests active during the primary nesting peak in 1965 (23 nests) was greater than the 1966 peak (20 nests), there were more nests concurrently

	IN A DELAWARE WOODEO1, 1903-1900										
	19) <mark>65</mark>		1	966			Totals			
		Per o	cent		Per	cent		Per	Per cent		
	Number	1*	2*	Number	1	2	Number	1	2		
Nests											
Incomplete	19	29		18	24		37	26			
Fate Unknown	4	6		8	11	_	12	8			
Active	43	65		50	66		93	65			
Successful	13	20	30	22	29	44	35	25	38		
Total Nesting Attempts**	66	_		76	_		142	_			
Cause of Failure											
Predation	30		70	19		38	49		53		
Weather	0	_		4		8	4		4		
Desertion	0	—	—	5		10	5	_	5		

Analysis of 142 Nesting Attempts of the Wood Thrush in a Delaware woodlot, 1965–1966

TABLE 1

* 1, Per cent of total nesting attempts; 2, Per cent of active nests; ** Successful nests are included in active nests.

active over a longer portion of the breeding season in 1966. The 1966 secondary peak was more than double the 1965 peak, suggesting more renesting or double nesting.

Analysis of nesting attempts.—An analysis of the 142 nesting attempts is presented in Table 1. A "nesting attempt" includes incompleted nests, active nests (any nest having received one egg), and "fate unknown" nests (outcome could not be determined). Thirty-five (38 per cent) of the 93 active nests were successful (at least one young fledged); 37 nests were incomplete and 12 nests were classified as "fate unknown."

Nice (1957) summarizing 7,788 nests for 24 studies found that success rate of open nests of altricial birds in the North Temperate Zone ranged from 38 to 77 per cent, averaging 49. Potter (1915) reported tree and bush nesters to have 43 per cent nest success. Kendeigh (1942) reported a 63 per cent success for 16 Wood Thrush nests observed during the period 1921–1939. Brackbill (1958) found 17 of 26 active nests (65 per cent) successful, with desertion, storms, predation and the intrusion of the Brownheaded Cowbird (*Molothrus ater*) affecting success.

In the present study, nest failures were attributed to predation, weather, and desertion. From examination of disturbed nests and the presence of egg remains, 49 nests were listed as destroyed by predators. Strong winds caused the loss of four nests and five other active nests were deserted.

	DISTR	ibe from	FOR	ACTIVE	Nests, 1	965–1966			
	Successful Nests		Unsuccess- ful Nests		Total Nests		Probability of Success in per cent		
Month *	1965	1966	1965	1966	1965	1966	1965	1966	(Both Years)
May	5	10	23	15	28	25	18	40	28
June	6	6	6	8	13	14	54	43	48
July	1	6	1	5	2	11	50	55	54
Totals	13	22	30	28	43	50	30	44	38

DISTRIBUTION OF WOOD THRUSH NEST SUCCESS BY YEAR AND MONTH

* Nest assigned to month in which first egg laid.

Probable avian predators on Wood Thrush eggs and young included the Common Grackle (Quiscalus quiscula), Blue Jay (Cyanocitta cristata) and Robin (Turdus migratorius). On one occasion a Blue Jay was observed taking a Wood Thrush egg from a nest. A Robin was flushed from another nest containing freshly punctured eggs.

Sizable populations of the eastern gray squirrel (Sciurus carolinensis) (three per acre) and the southern flying squirrel (Glaucomys volans) (two per acre) were present on the study area. These animals are thought to have destroyed some nests.

FACTORS ASSOCIATED WITH NEST SUCCESS

The success of active nests was related to advance of the breeding season (month), plant species in which the nest was located, height of nest above ground level, and vegetational type. The lack of Brown-headed Cowbird parasitism may have contributed to nest success. The inevitable disturbance caused by the investigators is acknowledged but the extent to which this disturbance affected success is unknown.

Advance of the season.-The probability of nest success increased from one month to the next as the season progressed (Table 2). For both years combined, success of nests initiated in June and July was considerably greater than success of nests started in May. Nest success in June 1965, however, was slightly higher than success in July.

Plant species in which nest located.-Wood Thrush nest success apparently was associated with the plant species in which the nest was located. Seventeen plant species were used as nesting sites for the 93 active nests (Table 3). Plants of five species, including two shrubs; arrowwood (26 nests), spicebush (11 nests), and three saplings, black gum ($N\gamma ssa \ sylvatica$) (14

Distribution	of W	UOD BY	Thrus Mon	511 NF FII, 19	еят S 965—1	uccess 966	in I	PLAN	t Spe	CIES		
		May	*	_	June			July	7	,	Totals	5
Plant Species	A	S	% S	A	S	% S	A	S	% S	A	S	% S
Shrubs												
Arrowwood	18	5	28	5	1	20	3	3	100	26	9	35
Spicebush	6	2	33	4	2	50	1	1	100	11	5	45
Black haw	2	0		_	_		1	1		3	1	33
Sweet pepperbush		_		_	_		1	1		1	1	100
Buttonbush	_			1	0		_	_		1	0	0
Saplings												
Black gum	4	1	25	7	4	57	3	1	33	14	6	43
Red maple	9	3	22	1	0	0	-	_	_	10	2	20
Flowering dogwood	4	1	25	3	2	67	1	0	0	8	3	38
American beech	3	1		1	1		_	_		4	2	50
Blue beech	2	1		_	_		1	0		3	1	33
Sweet gum	1	0		2	0		_	_		3	0	0
Black oak	_	_		2	2		1	0		3	2	67
Black cherry	1	1		-	—		1	0		2	1	50
Pignut hickory	—			1	1		_	_		1	1	100
White oak	1	0		—	_		_	_		1	0	0
Magnolia	1	0		_			_	-		1	0	0
ines												
Japanese honevsuckle	1	1		_			_	_		1	1	100

Distribution	OF	WOOD	THRUSH	Nest	SUCCESS	1N	Plant	Species
		ВY	Month,	1965-	-1966			

* A = Number of active nests; S = Number of successful nests; % S = Per cent successful.

nests), red maple (10 nests) and flowering dogwood (eight nests) were used for 69 of the nesting sites. Of these five species, spicebush and black gum were most often associated with successful nesting attempts.

Nest height.-Nest heights above ground level, grouped into four categories for comparative purposes are given in Table 4. Nest success was inversely proportional to nest height; the greatest success (53 per cent) occurred in the lowest nest-height class and the least success (15 per cent) in the highest nest-height class. The two lower height divisions span the usual heights of shrubs while the higher divisions are more representative of the saplings.

Vegetational type .- Over the two year period the ratios of active to successful nests in the two vegetational types were similar. In the upland type 22 of 54 active nests were successful and in the lowland type 13 of 39 were successful for ratios of 2.5:1 and 3.0:1, respectively.

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				AND N	IONTII	, 1905–	1900					
			Ne	st Heig	hts Ab	ove Gro	und—-(nearest	: 0.5 ft)		
Month	<	< 5.5 *			5.5-8.5	5		9-16			16.5-2	25
	A	S	% S	А	S	% S	Α	S	% S	A	S	% S
May	19	8	42	20	6	30	8	1	13	6	0	0
June	6	3	50	11	6	55	4	2	50	6	2	33
July	2	2	100	6	4	67	4	1	25	1	0	0
Totals	27	3	48	37	16	43	16	4	25	13	2	15

DISTRIBUTION	OF	Wood	THRUSH	Nest	Success	ВY	Nest	Height
		AND	Month	, 1965	-1966			

* A = Number of active nests; S = Number of successful nests; % S = Per cent successful.

Influence of Brown-headed Cowbirds on success.—While other authors (Weaver, 1939; Brackbill, 1958; and Friedmann, 1963) report that cowbird parasitism is a factor in the nesting success of the Wood Thrush, no such parasitism was observed in this study. Cowbirds were present and were found to have laid eggs in the nests of the Red-eyed Vireo (Vireo olivaceus), Rufous-sided Towhee (Pipilo erythrophthalmus), Yellowthroat (Geothlypis trichas), and Kentucky Warbler (Oporornis formosus). Friedmann (ibid.) lists the recorded frequency of parasitism for these four species as 875, 300, 250 and 150, respectively. In contrast, only 75 records have been noted for the Wood Thrush. Perhaps the availability of the more "preferred" host species tended to exclude the use of less frequently parasitized hosts such as the Wood Thrush.

Interactions.—Nest success did not increase progressively during the season for any given plant species, except spicebush, because usage of certain species changed with the season. Red maple and spicebush were used mostly in early season, black gum in mid-season, and arrowwood supported a disproportionately higher number of successful nests in July.

Monthly differences in success may be partially explained by: (1) the phenological changes of the vegetation are such that foliage is denser and affords more cover for nest concealment later in the season, (2) the amount of parental care available per nestling is probably greater in July during re-nesting when clutches are smaller than during early nesting attempts, and (3) the functional response of predators (Leopold, 1933; Holling, 1961) is to destroy a higher proportion of prey (eggs or young in nests) when more are available. These variables, singly or in combination, may explain the higher nest losses in May and lower losses in June and July when fewer nests were active.

Of the five predominant plant species used, success was lowest in red

	Clutci	H SIZE OF B	74 Completed Wood Thru y Month for 1965–1966	SII CLUTCHES		
Faar por			Number of clutches by month for both years			
clutch		May	June	July	Totals	
2		0	6	3	9	
3		13	14	10	37	
4		24	2	0	26	
5		2	0	0	2	
Totals		39	22	13	74	
Average o	elutch size	3.7	2.8	2.8	3.3	

maple. This low success appeared related to the high average nest-height and the early average time of the season for nests in this plant species. In addition, nests at these heights before complete development of foliage, were quite conspicuous, at least to the investigators. Nine of the 10 active nests in red maple were initiated in May and six of the 10 nests were over nine feet above ground level. Although Weaver (in Bent, 1949) states that "there seems to be little choice in selecting the kind of tree, shrub or vine used," Preston and Norris (1947) theorize that "we are so accustomed to thinking of tree-tops as a relatively safe place for birds that it may be difficult to envisage them as a highly dangerous place, only to be used as a last resort." Our data tend to support the latter idea with respect to the sapling understory.

Nest success varied among nest heights between months of the breeding season. The two lower nest-height classes show increasing nest success from May through July, but the two higher nest classes show greater nest success in June than in May or July. The two trends are most pronounced in the extreme height classes, i.e., < 5.5 feet and 16.5-25 feet.

PRODUCTIVITY

Clutch size .-- Mean clutch size decreased as the breeding season progressed (Table 5). Four-egg clutches were common in May and absent in July. Average clutch size was determined from 74 completed clutches. Twoegg clutches and many three-egg clutches in June and July were most likely from re-nesting pairs as success was low in May. Only one adult, out of 14 Wood Thrushes captured in late June was a new unbanded bird, compared to 16 new birds of 26 captured (62 per cent) in May and early June, indicating that the breeding population had stabilized, and the June-July nests were not likely built by newly arrived birds.

An effort was made to determine the extent of double nesting among Wood Thrush in the study woodlot. Nine adult Wood Thrushes which were thought to be residents of the woodlot because they were banded during a previous breeding season or because they were caught repeatedly during 1966, were color marked and observed when possible. Only one color marked bird was observed at a nest; this bird, a female banded the previous August, was observed three times at or near a nest which contained five eggs. The nest blew down during the period 7-11 June and the marked bird built another nest nearby on 13 June, from which three birds were fledged between 12-15 July. Brackbill (1958) observing nine color banded pairs, found two broods per year to be the rule near Baltimore, Maryland. Weaver (1939) recorded a second successful nesting for a color marked pair near Ithaca, New York. Eaton (1914) states that the eggs are usually laid from 17-30 May but later sets are frequently found as late at 25 June and 10 July. Forbush (1927) states: "One brood yearly in New England though said to rear two in the west and south." Sprunt and Chamberlain (1949) reporting for South Carolina indicate the interval between the two broods is very brief. One record, for example, makes note of young leaving a nest on 6 June, while one parent was still feeding them and of the other adult carrying nesting material two days later and settling into the completed second nest by 11 June.

Success of eggs and nestlings.—Fifty-two per cent of the 276 Wood Thrush eggs hatched (Table 6). On the basis of the total eggs hatched, 65 per cent fledged. However, on the basis of total eggs laid, only 33 per cent fledged. By considering both ways of calculating success, a more exact estimate can be obtained for nests in which there is only partial success of a clutch but in which the nest is considered successful.

Other workers have reported varying rates of nest success with which bur findings are generally in accord. In 29 studies involving 21,951 eggs, fledging success of altricial birds ranged from 22–70 per cent, averaging 46 (Nice, 1957). Weaver (1939) found that of 51 eggs laid in 15 Wood Thrush nests, 33 (65 per cent) produced young, and 22 fledged. This was a survival of 43 per cent of the eggs laid and 66 per cent of the young hatched. Brackbill (1958) observed that of 44 eggs laid in 15 nests, 39 hatched (89 per cent), and 35 young fledged (80 per cent of eggs laid and 90 per cent of the eggs which hatched). Kendeigh (1942) reported that of 14 Wood Thrush eggs laid in 10 successful nests, 79 per cent hatched, while 58 per cent of the eggs which hatched, survived to fledge. Kendeigh further stated that in successful nests 46 per cent of the eggs laid became fledglings, but in successful and unsuccessful nests combined only 29 per cent of the eggs laid developed into fledglings. Longeore and Jones

Fate of Wood Thrush Eccs and Nestlings from 93 Active Nests, 1965–1966									
	1965	1966	Total						
Aetive nests	43	50	93						
Eggs laid	124	152	276						
Mean/Active nest	2.9	3.0	3.0						
Eggs hatched	54	88	142						
Mean/Active nest	1.3	1.8	1.5						
Young fledged	27	65	92						
Mean/Active nest	.6	1.3	1.0						
Eggs lost									
Infertile or addled	5	3	$(3)^{1}$						
Predation	63	43	106 (38)						
Weather	0	9	9 (3)						
Desertion	0	5	5 (2)						
Unknown	2	4	6 (2)						
Nestlings lost									
Predation	26	13	39 (27)						
Weather	0	8	8 (6)						
Unknown	1	2	3 (2)						

				Т.	ADLL	0			
Fate	OF	WOOD	Thrus	Н	Eccs	AND	Nestlings	FRO M	93
		1	ACTIVE	Ν	ests,	1965-	-1966		

TADLE 6

¹ () Per cent.

Reproductive success also may be expressed as the mean number fledged per either active or successful nest. In this study an average of 2.6 young was fledged from 35 successful nests and an average of 1.0 young from 93 active nests (which includes both successful and unsuccessful nests). Regardless of various interactions affecting success, egg and nestling attrition in successful nests is not extensive. Of the 111 eggs produced in 35 successful nests, 92 eggs (83 per cent) hatched and subsequently fledged.

Predation was the largest mortality factor, apparently causing a loss of 38 per cent of the total eggs laid and 27 per cent of the nestlings which hatched. In open nesting songbirds over three-quarters of the losses of eggs and young are due to predation (Lack, 1954).

SUMMARY

A study of the reproductive success of the Wood Thrush in a suburban area was eonducted near Newark, Delaware during 1965-1966.

Nesting peaks occurred in the last week of May and in the second week of July. A total of 142 "nesting attempts" was recorded with 93 active nests; 35 (38 per ecnt) of which were successful. Destruction of 49 nests (58 per cent) was attributed to predators. Inclement weather and descriton eaused some nest failures.

In general, the greatest nest success was associated with (a) late season nests

(June and July), with (b) spicebush and black gum vegetation, and with (c) the lower heights of nests above ground level (below 8.5 feet). Low nest success was associated with May nesting, red maple, and heights above nine feet. There was little difference in success between the two vcgetational types: upland and lowland.

Arrowwood, black gum, red maple, spicebush, and flowering dogwood were the most commonly used plant species of the 17 used to support active nests.

Mean clutch size decreased from May to July. The average clutch size was 3.3 eggs per nest with clutches ranging from 2–5 eggs. Thirty-three per cent of the total eggs laid, hatched while 65 per cent of the hatched birds survived to leave the nest.

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